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Seasonal Abundances of Euthecosomatous Pteropods and Heteropods from Waters Overlying San Pedro Basin, California

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Abstract. Ten species of euthecosomatous pteropods and five heteropod species were recorded from replicated oblique plankton tows to a target depth of 300 m taken with an open, 2 m diameter ring net (3 m^2 mouth opening) during 13 monthly cruises from April 1989 to April 1990 in San Pedro Basin, California. Six species of euthecosomes and one atlantid heteropod species were sufficiently numerous in the samples to allow assessment of seasonal patterns. The most abundant euthecosome (*Limacina helicina*) and heteropod (*Atlanta californiensis*) are epipelagic species that belong to the Transitional Faunal Province in the North Pacific. The highest densities of both species occurred during the summer, coinciding with the strongest seasonal flow of the California Current and Southern California Eddy. Conversely, during the winter when flow of these currents was weakest, the lowest densities of these species were recorded. Three euthecosome species (*Creseis virgula, Limacina bulimoides,* and *Cavolinia inflexa*) are warm water (tropical and subtropical) epipelagic species, although the latter two are most abundant in Central waters. Whereas *C. inflexa* showed no pattern of seasonal abundance, *C. virgula* and *L. bulimoides* had increased densities in the summer, corresponding to the time of maximal Southern California Countercurrent flow. Lastly, two euthecosome species (*Limacina inflata* and *Clio pyramidata*) are warm water, mesopelagic species that undergo nocturnal vertical migration into epipelagic waters. Maximal densities of *L. inflata* were recorded during the winter, which corresponds to a secondary peak in flow strength of the California Current and surfacing of the California Undercurrent. There was no seasonal pattern of abundance for *C. pyramidata.*

INTRODUCTION

The euthecosomatous pteropods and heteropods comprise morphologically distinct and distantly related groups of holoplanktonic gastropod mollusks. The majority of heteropods have cosmopolitan distributions, although they normally are not abundant and are limited primarily to tropical and subtropical waters. Like the heteropods, many of the euthecosomes are cosmopolitan and are tropical and subtropical, although some species are found in Arctic and Antarctic waters (Lalli & Gilmer, 1989). The euthecosomes, however, are generally more abundant than the heteropods and can be highly numerous, occasionally attaining densities in excess of 100,000 m^{-3} (McGowan, 1968)

From the California Current region off the west coast of the United States and Baja California, Mexico, distributions and abundances of euthecosomes and heteropods were reported by McGowan (1967) as part of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) atlas series. These maps were based on oblique tows taken with standard CalCOFI 1 m plankton nets at stations located on the CalCOFI sampling grid during six cruises between November 1949 and October 1952.

The present study represents the first report on euthecosomes from the California Current since the Ph.D. thesis of McGowan (1960), the CalCOFI Atlas (McGowan, 1967), and related papers (McGowan, 1963, 1968, 1971). McGowan also treated the heteropods in his 1967 atlas, as well as including certain species in two other papers (McGowan, 1971; Fager & McGowan, 1963). Heteropods from the California Current region have been the subject of several studies (Dales, 1953; Seapy, 1974, 1980; Seapy & Richter, 1993).

Here we examine the species composition and abundances of euthecosomes and heteropods over a 13 month period from waters overlying the San Pedro Basin off southern California. These data enabled us to hypothesize seasonal patterns of abundance, which we have attempted to relate to the geographical and depth distributions and to seasonal differences in flow of the California Current, Southern California Eddy and Countercurrent, and the California Undercurrent.

MATERIALS AND METHODS

Thirteen consecutive monthly cruises were conducted aboard the R/V *Yellowfin,* Southern California Marine Institute, from April 1989 to April 1990 in waters overlying the San Pedro Basin, located between the Palos Verdes Peninsula and Santa Catalina Island (Figure 1). The expanded continental shelf off southern California (termed

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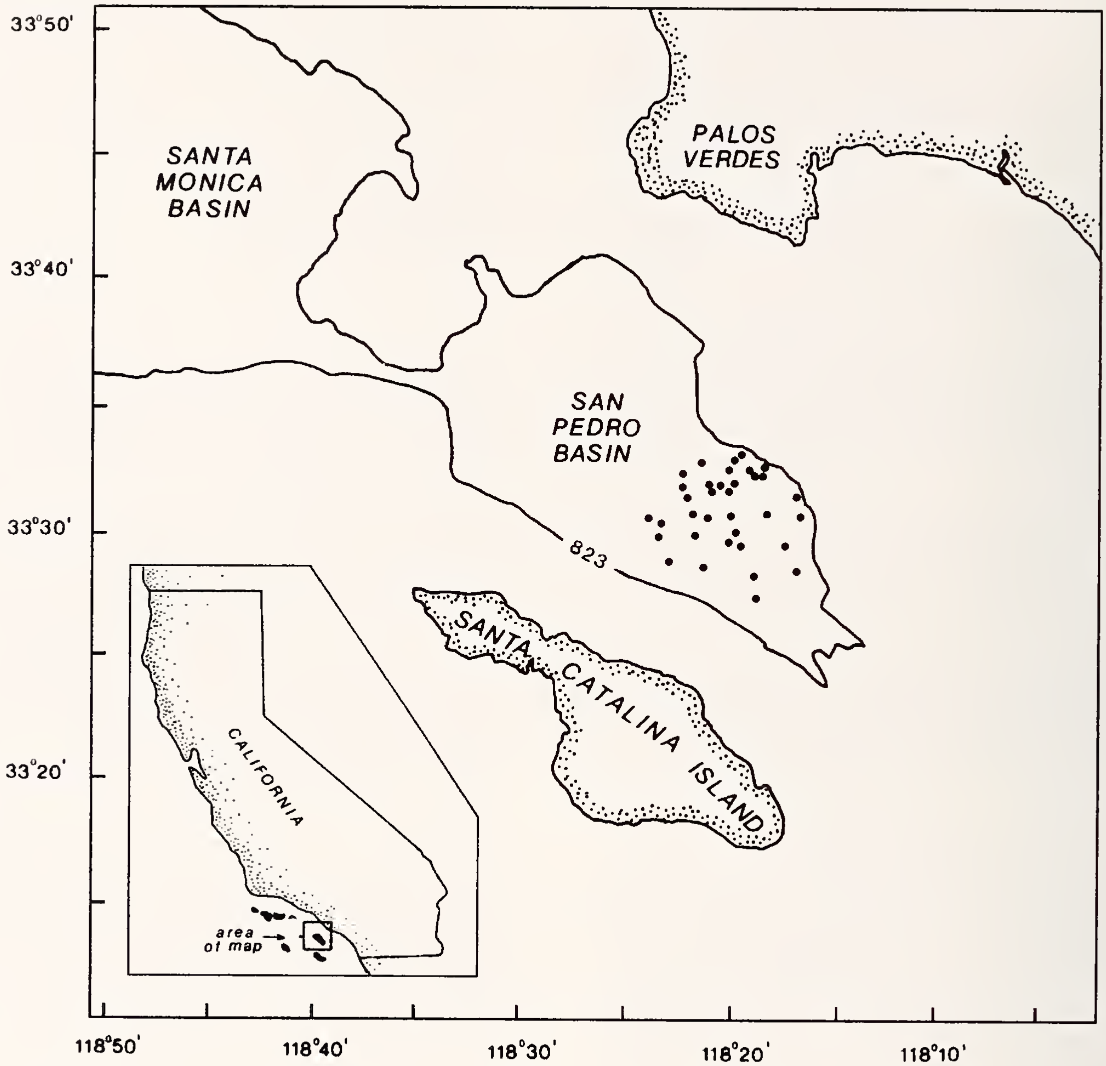

Figure 1. Locations of starting positions for plankton tows taken in San Pedro Basin waters over the 13-month study period. All tows were taken in the southeastern portion of San Pedro Basin, where bottom depths exceeded 823 m (indicated by the contour lines on the plot).

the Southern California Borderland) includes a series of nearshore, intermediate, and offshore basins. The San Pedro Basin is the deepest of the three nearshore basins (the other two being the Santa Monica and Santa Barbara Basins) and has a maximal depth of 912 m (Lavenberg & Ebeling, 1967). The area covered by the Borderland extends in a broad arc southeastward from Point Conception to northern Baja California, and is commonly referred to as the Southern California Bight.

All tows were taken with an open ring net having a mouth opening 2 m in diameter and 3 m^2 in area. The net was 9 m in length and was a cylinder-cone design, with the cylindrical portion 4.5 m in length. The net was constructed of 505 μm mesh Nytex cloth. Towing bridles were attached to opposite sides of the net ring, with the result that the mouth opening was nearly unobstructed during tows. This bridle arrangement and the large mouth size of the net were designed to reduce the potential problem of net avoidance, which was demonstrated for euthecosomes (McGowan & Fraundorf, 1966) and heteropods (Seapy, 1990a) using plankton nets of different sizes. Since the metamorphosed larvae of euthecosomes and heteropods are mostly larger than about 0.5 mm, juvenile and adult specimens were retained in the net while most larvae were capable of passing through the net mesh and may or may not have been retained. For this reason, our sample counts only included juvenile and adult individuals.

During each monthly cruise, five oblique tows (except in May and June with four and six tows, respectively) were taken to a target depth of 300 m during daylight hours. This depth was chosen based on the findings of McGowan (1960) that the vertical ranges of most euthecosomes are limited to the epipelagic zone, and those that range into the mesopelagic zone decrease in abundance substantially below about 300 m. In his 1968 paper, McGowan listed most species as epipelagic, although the daytime ranges of several extended into the mesopelagic or were mesopelagic, and one, *Clio polita* (Pelseneer, 1888), was bathypelagic. In the nearshore Santa Barbara and San Pedro Basins, the epipelagic zone ranges to 150 m, while the mesopelagic zone lies between 150 m and about 600 m, with the upper mesopelagic zone extending to about 350–400 m (Paxton, 1967; Ebeling et al., 1970). Thus our oblique tows taken to a depth of 300 m in San Pedro Basin extend through the epipelagic and most of the upper mesopelagic zones.

A Benthos Time-Depth Recorder (TDR) was secured to the bottom of the net ring. After completing a series of oblique tows, the maximal depths reached by the net were determined from the TDR. Despite the fact that there was no means of continuously monitoring the depth of the net, we were reasonably successful in approximating the 300 m depth (actually achieving this depth in 11 tows). We employed the following method that required adjusting the length of cable paid out during each tow. As the net descended, the angle of the towing cable was measured relative to the vertical using a handheld wire angle indicator. The length of cable to be paid out was then calculated by dividing the target depth of 300 m by the cosine of the wire angle. Maximal depths of the 65 tows taken during the study ranged from 202 m to 400 m. Of these tows, 39 (three from each month) were selected. Except for a 400 m tow that had to be used in May, maximal tow depths ranged from 280 to 346 m. The average depth was 315.6 m, and the upper and lower 95% Confidence Interval was 308.7 to 322.5 m, a range of only 13.8 m. During each tow, ship speed was maintained at 1 knot by running on only one of the two engines. Each tow took about 40 to 45 minutes, with the net reaching its maximal depth within approximately 20 minutes.

The volume of water filtered during each tow was determined using a T.S.K. Model WA-200 Flow Meter, attached to the top center of the mouth opening of the net. The filtered volume was calculated based on the number of flow meter revolutions, the calibrated distance traveled by the net per flow meter revolution (0.15 m per revolution), and the mouth area of the net (3.0 m^2). Filtered volumes averaged 8873 m^3 and ranged from 6445 m^3 to 14,207 m^3. Species abundances are reported here in numbers per 10,000 m^3, which is close to the average filtered volume of water.

All samples were placed into 1-gallon glass jars and fixed in 3% Borax-buffered seawater formalin (pH 8.0). To assure collection of both abundant and rare species, the entire sample was sorted for euthecosomes and heteropods except for the March samples. Due to the extremely large sample volumes collected during that month, the samples were split to one-fourth of their initial volumes using a Folsom Plankton Splitter.

Species counts and identifications were made using a Wild M5 dissecting microscope. Species identifications of the euthecosomes were based on Bé & Gilmer (1977), while those of the heteropods followed Okutani (1961), Seapy (1974), Seapy & Richter (1993), and Richter & Seapy (1999). For certain pteropod and heteropod taxa, van der Spoel (1967, 1976) and van der Spoel et al. (1997) used the infraspecific category of "forma." However, we have chosen not to follow this infraspecific designation in agreement with the above-mentioned authors. Classification of *Diacria* species was reviewed and revised by Bontes & van der Spoel (1998), but our initial identification of specimens as *D. trispinosa* (de Blainville, 1827) remained unchanged after we consulted this paper.

Two geographically distinct varieties of *Limacina helicina* (Phipps, 1774) were recognized by McGowan (1963) from the North Pacific based on differences in shell morphology: a high-spired form with growth striae (var. A) and a low-spired form without striae (var. B). McGowan expressed this shape difference numerically as the ratio of shell height to diameter, which averaged 0.97 for var. A and 0.77 for var. B. The geographical distributions of these two varieties largely correspond to the distributions of two of the water masses of the North Pacific; var. A in the Subarctic Pacific and var. B in the Transition Zone. Specimens from the present study corresponded in appearance and shape (height to diameter ratio average = 0.70; range = 0.61–0.79; n = 15) to variety B (Cummings, 1995). Interestingly, the average value of 0.70 was somewhat lower than that (0.77) found by McGowan, which could be a reflection of the more southerly location of our study area in California Current waters.

The identity of specimens assigned to two species, *Creseis virgula* (Rang, 1828) and *Clio pyramidata* Linnaeus, 1767, was somewhat problematical. Bé & Gilmer (1977) recognized three subspecies of *C. virgula: virgula* (Rang, 1828), *conica* Eschscholtz, 1829, and *constricta* (Chen & Bé, 1964). These authors based subspecific differences on curvature of the shell and the presence of an expansion or constriction between the juvenile and adult shell. Only the first two subspecies are valid, however, since Wells (1977) showed that *C. virgula constricta* is the juvenile stage of *Cuvierina columnella* (Rang, 1827). In the present study only specimens corresponding to *C. virgula virgula* were collected. Six "formae" of *Clio pyramidata* were recognized by van der Spoel et al. (1997); the specimens collected in our study most closely resemble *C. pyramidata* forma *lanceolata* Linnaeus, 1767.

RESULTS

Ten species of euthecosomatous pteropods, belonging to two families (the Limacinidae and Cavoliniidae), were

Table 1

Ranked order of the averaged mean monthly densities (expressed as numbers per 10,000 m^3 and as percentages) for species of euthecosomatous pteropods and heteropods collected from San Pedro Basin between April 1989 and April 1990.

Species	Mean density (No.·10,000 m^{-3})	Percent
Euthecosomes:		
Limacina helicina	415.1	39.23
Creseis virgula	227.7	21.52
Limacina inflata	152.8	14.44
Clio pyramidata	51.3	4.85
Limacina bulimoides	8.9	0.84
Cavolinia inflexa	4.5	0.42
Clio cuspidata	0.3	0.03
Diacria trispinosa	0.1	0.01
Cuvierina columnella	<0.1	<0.01
Cavolinia tridentata	<0.1	<0.01
Heteropods:		
Atlanta californiensis	196.8	18.60
Pterotrachea coronata	0.3	0.03
Carinaria japonica	0.1	0.01
Atlanta peroni	0.1	0.01
Firoloida desmaresti	0.1	0.01
Total	1058.1	100.00

identified from the samples collected over the course of the study. The limacinids were represented by three species of *Limacina* (*L. bulimoides* [d'Orbigny, 1836], *L. helicina,* and *L. inflata* [d'Orbigny, 1836]). The cavoliniids included seven species belonging to three subfamilies: three Cavoliniinae (*Cavolinia inflexa* [Lesueur, 1813], *C. tridentata* [Neibuhr, 1775], and *Diacria trispinosa*), three Clioninae (*Clio cuspidata* [Bosc, 1802], *C. pyramidata,* and *Creseis virgula*), and one Cuvierininae (*Cuvierina columnella* [Rang, 1827]).

The mean monthly densities of four euthecosomes contributed nearly 80% of the total mean density for all euthecosomes and heteropods (Table 1). In order of decreasing importance, they were *Limacina helicina* (415·10,000 m^{-3} or 39%), *Creseis virgula* (228·10,000 m^{-3} or 22%), *Limacina inflata* (153·10,000 m^{-3} or 14%), and *Clio pyramidata* (51·10,000 m^{-3} or 5%). Two species (*Limacina bulimoides* and *Cavolinia inflexa*) had monthly mean densities that averaged 9·10,000 m^{-3} (or 0.8%) and 5·10,000 m^{-3} (or 0.4%), respectively, while two species (*Clio cuspidata* and *Diacria trispinosa*) represented less than 1·10,000 m^{-3} each (0.03 and 0.01%, respectively). The remaining two species (*Cuvierina columnella* and *Cavolinia tridentata*) were each collected only once during the entire sampling period.

Limacina helicina had a maximal mean density of 2267·10,000 m^{-3} in July, with moderately high numbers (between about 350 and 900·10,000 m^{-3}) from June to October (Figure 2). However, from November to the end of the study, monthly mean densities were less than 90·10,000 m^{-3}.

Creseis virgula rose steadily in abundance from June to August, when its peak mean density of 1626·10,000 m^{-3} was recorded (Figure 2). Densities then declined dramatically in September (213·10,000 m^{-3}), and subsequent months recorded low to very low levels, except for a small increase in December.

Limacina inflata had a maximal mean monthly density of 723·10,000 m^{-3} in December (Figure 2), which was then followed, except for the inexplicably low mean density recorded for January, by declining numbers (546 and 212·10,000 m^{-3}) in February and March, respectively. Moderately low to low numbers were recorded during the other months of the study.

Clio pyramidata was collected during every month of the study (although in very low numbers in May 1989) and was absent from only three tows (Figure 2). There was no evident seasonal pattern to the data. Moderate numbers (means of 72 to 107·10,000 m^{-3}) were recorded for the summer months, preceded by 2 months of very low densities (less than 3·10,000 m^{-3}). The highest mean density (125·10,000 m^{-3}) occurred in February, and abundance in April was in the range of the summer months.

Limacina bulimoides was most abundant (monthly densities greater than about 5·10,000 m^{-3}) during only 3 months (June, August, and December) of the study (Figure 2), and it was either absent or occurred in low densities during the intervening period.

Cavolinia inflexa had very low monthly densities ($<$ 1·10,000 m^{-3}) during the first 6 months of the study (Figure 2). However, two periods of somewhat elevated numbers followed from October to December and again in March and April, at which time the highest monthly mean density (23·10,000 m^{-3}) was recorded.

Five species of heteropods, belonging to three families (Atlantidae, Carinariidae, and Pterotracheidae) were identified: two atlantids (*Atlanta californiensis* Seapy & Rich-

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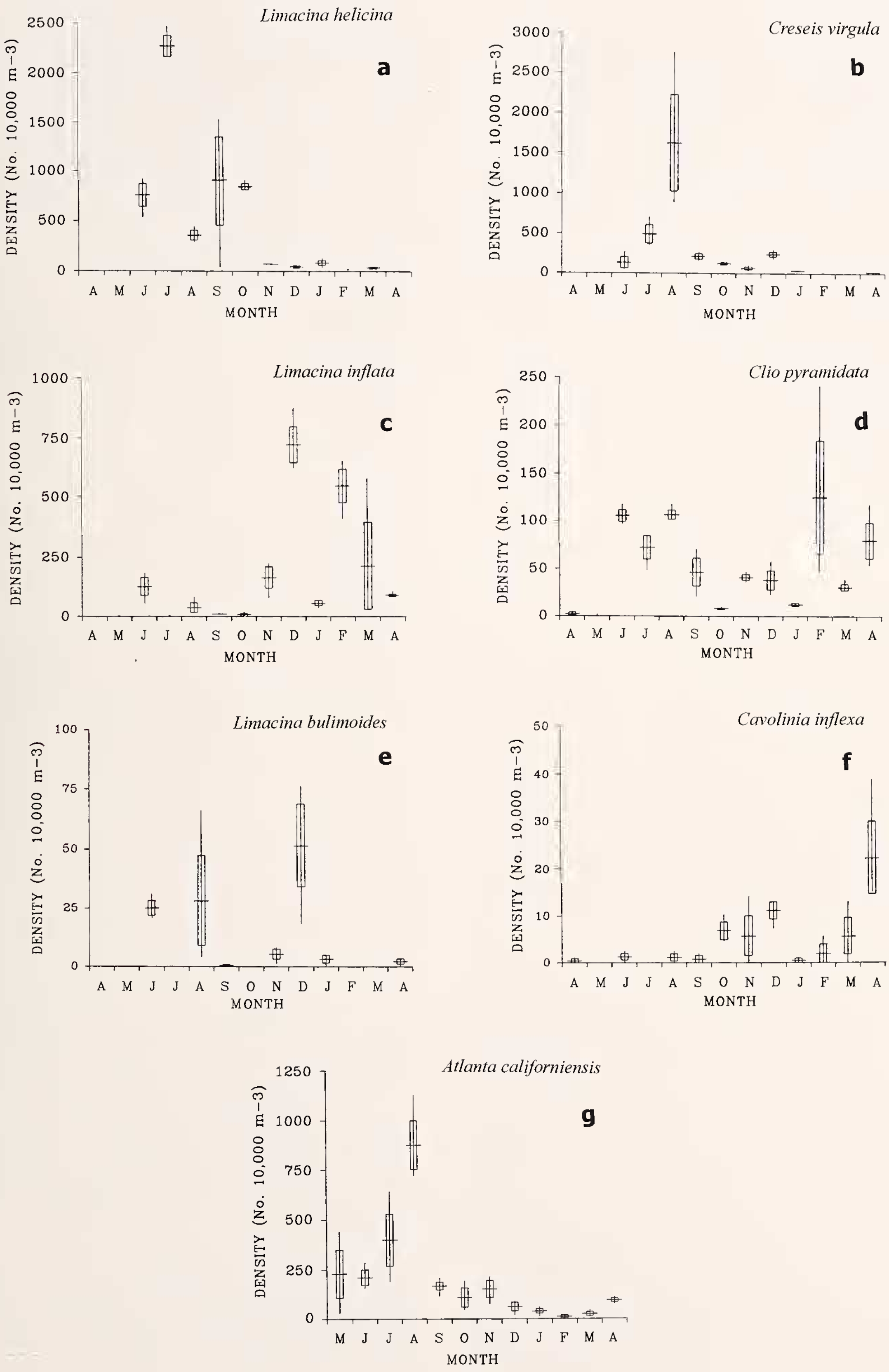
Figure 2. Monthly densities (numbers per 10,000 m^3) of euthecosomatous pteropods and heteropods from epipelagic and upper mesopelagic depths in waters overlying San Pedro Basin. Mean monthly densities were calculated from three replicate oblique tows taken with a 3 m^2 ring net to a target depth of 300 m from April 1989 to April 1990. Each monthly plot includes a horizontal bar (mean density), vertical bar (range of densities among the replicate tows), and rectangular box (plus and minus one standard error of the mean density).


Limacina helicina
a
DENSITY (No. 10,000 m−3)
2500
2000
1500
1000
500
0
A M J J A S O N D J F M A
MONTH
Creseis virgula
b
DENSITY (No. 10,000 m−3)
3000
2500
2000
1500
1000
500
0
A M J J A S O N D J F M A
MONTH
Limacina inflata
c
DENSITY (No. 10,000 m−3)
1000
750
500
250
0
A M J J A S O N D J F M A
MONTH
Clio pyramidata
d
DENSITY (No. 10,000 m−3)
250
200
150
100
50
0
A M J J A S O N D J F M A
MONTH
Limacina bulimoides
e
DENSITY (No. 10,000 m−3)
100
75
50
25
0
A M J J A S O N D J F M A
MONTH
Cavolinia inflexa
f
DENSITY (No. 10,000 m−3)
50
40
30
20
10
0
A M J J A S O N D J F M A
MONTH
Atlanta californiensis
g
DENSITY (No. 10,000 m−3)
1250
1000
750
500
250
0
M J J A S O N D J F M A
MONTH

ter, 1993, and *A. peroni* Lesueur, 1817), one carinariid (*Carinaria japonica* Okutani, 1955), and two pterotracheids (*Firoloida desmaresti* Lesueur, 1817, and *Pterotrachea coronata* Niebuhr [ms. Forskål, 1775]).

Atlanta californiensis accounted for 99.7% of the total mean heteropod density and, after the euthecosomes *Limacina helicina* and *Creseis virgula,* ranked third in total mean density for all euthecosome and heteropod species (197·10,000 m^{-3}) (Table 1). It increased in abundance from 230 and 211·10,000 m^{-3} in May and June, respectively, to a peak of 882·10,000 m^{-3} in August (Figure 2). After August it declined sharply to 167·10,000 m^{-3} in September, after which abundances declined steadily to a low of 6·10,000 m^{-3} in February.

The most numerous of the remaining heteropod species, *Pterotrachea coronata,* had a mean monthly density of only 0.3·10,000 m^{-3} (Table 1), with the greatest number of individuals (five) collected in October 1989 and two individuals from each of three other months (June, December, and January). The remaining heteropods were collected in extremely low numbers: three *Atlanta peroni* (in June 1989 and January 1990), three *Firoloida desmaresti* (in August 1989), and two *Carinaria japonica* (in March 1990).

DISCUSSION

Surface flow over the Southern California Borderland is dominated by the Southern California Eddy, which is a counterclockwise-flowing extension of the California Current. The Eddy forms when the California Current turns shoreward in a broad arc onto the Borderland, mostly to the south of Cortes Bank (at about 32°30′N latitude, 119°15′W longitude). Then, upon approaching the coast, the Eddy turns and flows northwestward as the Southern California Countercurrent. Surface waters in the California Current and the Southern California Eddy have flow maxima in the late summer and minima in the winter, at which time the Southern California Eddy weakens or breaks down altogether (Hickey, 1979, 1993). Subsurface flow (below about 200 m) over the Borderland is dominated by the northwesterly flowing California Undercurrent, which is formed by submergence of Equatorial Pacific waters off southern Baja California (Reid et al., 1958; Emery, 1960; Hickey, 1992). The Undercurrent has a seasonal flow maximum in the summer (like the California Current), a secondary maximum in the winter when it surfaces (Lynn & Simpson, 1990), and a minimum in the spring (Hickey, 1993).

Images of satellite-derived sea surface temperatures covering the region from 20°N to 40°N and 110°W to 135°W (National Oceanographic and Atmospheric Administration, National Weather Service) were analyzed for the first 12 months of the study (Cummings, 1995). Six of the images exactly matched the dates of sampling, whereas the other six were within 1 or 2 days of the sampling dates. These images indicated that during the period of our study surface flows were in agreement with the long-term pattern off the west coast of the United States described above. The California Current strengthened from spring through summer of 1989, as demonstrated by progressive equatorward bending of surface isotherms, and reached a maximum in September and October. As the surface flow strengthened through the summer, the Southern California Eddy became more prominent and also reached a maximum in September and October. By December, however, it had weakened substantially and it was gone in February.

Biogeographic patterns of a wide variety of taxa correspond with the major water mass distributions in the North Pacific (McGowan, 1986): Subarctic, Central North Pacific, Transitional, Equatorial, and Eastern Tropical Pacific. Waters overlying the Southern California Borderland are derived from the Subarctic, Central, and Equatorial Pacific waters (Reid et al., 1958; Hickey, 1992). In agreement with the "transitional" nature of the area, Ebeling et al. (1970) characterized the Southern California Bight as an area that supports a biogeographically heterogeneous fauna of fishes and invertebrates. The biogeographic affinities of the 10 euthecosomes and five heteropods recorded in this study were obtained from the literature and are summarized in Table 2.

Based on the above oceanographic features, three patterns of seasonal abundances can be hypothesized for the euthecosomes and heteropods recorded in San Pedro Basin. First, epipelagic Transitional species will have a seasonal maximum during the summer months, declining during the fall to a winter minimum. Second, warm water epipelagic species will be present in low abundances year-round, but will increase in abundance during the spring to summer period of strengthened Southern California Countercurrent flow. Third, warm water mesopelagic species will be present year-round, but will become more abundant during summer through winter months, with a winter peak when the California Undercurrent surfaces.

In the following discussion, comparisons between our density data and those of McGowan (1967) must be qualified because of differences in plankton net design, maximal tow depth, and diel period of sampling. The CalCOFI samples examined by McGowan were collected with a 1 m, conical plankton net having a 1 m diameter mouth opening and a length of 5 m. This net had a substantially smaller mouth area (0.785 m^{-2}) than ours (3.0 m^{-2}), a similar mesh size (0.55 mm vs. 0.51 mm), and a considerably shallower oblique tow depth (70 m during 1949 and 1950, and 140 m subsequently) than ours (300 m). Because the area of the mouth opening of our net was nearly four times that of McGowan's net, density data for those species capable of net avoidance conceivably represent underestimates in McGowan's data. Also, the substantial difference in maximal tow depth implies that comparisons between McGowan's daytime samples

Table 2

Geographical and daytime vertical distributions of euthecosome and heteropod species collected from San Pedro Basin. Based on the literature, the geographic distribution of each species in the North Pacific can be designated (after McGowan, 1974) as: Subarctic (SA), Central (C), Transitional (TR), Equatorial (EQ), Eastern Tropical Pacific (ETP), and warm water (WW). Except as noted, the latter category consists of cosmopolitan species that are broadly distributed through Central and Equatorial waters. Following the geographical and daytime distribution columns, the literature sources are given as: (1) Bé & Gilmer (1977), (2) Fager & McGowan (1963), (3) McGowan (1963), (4) McGowan (1968), (5) McGowan (1971), (6) Michel & Michel (1991), (7) Pafort-van Iersel (1983), (8) Seapy (1990b), (9) Seapy (unpublished), (10) Seapy & Richter (1993), (11) Wormelle (1962), (12) Wormuth (1981), (13) van der Spoel et al. (1997).

Species	Geographical distribution	Literature source	Daytime distribution	Literature source
1. Transitional epipelagic species:				
Euthecosomata—				
Limacina helicina var. B	TR	3	epipelagic	1, 4
Heteropoda—				
Atlanta californiensis	TR	10	epipelagic	9
Carinaria japonica	TR	5	epipelagic	9
2. Warm-water epipelagic species:				
Euthecosomata—				
Creseis virgula	WW	1, 2, 5	epipelagic	1, 4, 12
Limacina bulimoides	WW*	1, 2, 5	epipelagic	1, 4, 12
Cavolinia inflexa	WW*	1, 2, 5	epipelagic	1, 4, 12
Cavolinia tridentata	WW	1, 5	epipelagic	4
Cuvierina columenlla	WW	1	epipelagic	1, 4
Heteropoda—				
Atlanta peroni	WW	13	epipelagic	6, 8
Firoloida desmaresti	WW	13	epipelagic	8
3. Warm-water mesopelagic species:				
Euthecosomata—				
Limacina inflata	WW	1, 2, 5	mesopelagic	11, 12
Clio pyramidata	WW*	1, 2, 5	mesopelagic	4, 12
Clio cuspidata	WW	1	mesopelagic	12
Diacria trispinosa	WW	1, 5	mesopelagic	11
Heteropoda—				
Pterotrachea coronata	WW	13	mesopelagic	7, 9

* Highest abundance in Central waters (1, 2); present in low abundance or absent in Equatorial waters, especially in the Eastern Tropical Pacific (5).

and ours are problematical for species whose ranges extend into waters below his maximal tow depths. Nocturnal migrations have been documented for a number of lower epipelagic and mesopelagic species of euthecosomes (Wormuth, 1981; Wormelle, 1962) and heteropods (Pafort-van Iersel, 1983; Seapy, 1990b). Thus McGowan's nighttime tows are probably more comparable with our tows because nocturnal migrators from depths below the maximal depths of his tows were undoubtedly represented in his nighttime samples.

Transitional Epipelagic Species

Three species (*Limacina helicina* var. B, *Atlanta californiensis*, and *Carinaria japonica*) are included in this group (Table 2). Because the surface waters overlying the San Pedro Basin are primarily derived from the southward-flowing California Current, one would predict that the most abundant species in our study would be Transitional. In agreement, *L. helicina* and *A. californiensis* were the first and third most abundant species, respectively, in our study. However, *C. japonica* was surprisingly uncommon (only two specimens were collected in the entire study). Both *L. helicina* and *A. californiensis* exhibited abundance maxima in the summer and minima in the winter. McGowan (1967) recorded *L. helicina* in moderate to high densities in waters off central and southern California from April to August, although the period of highest abundance in our study was 2 months later (June to October). Because *A. californiensis* was not recognized at the time of McGowan's study, no comparisons with his records are possible.

Patterns of distribution and abundance of *Carinaria ja-*

ponica from Borderland and oceanic waters off southern California were studied by Seapy (1974). He found summer maxima and winter minima; thus supporting its classification as a Transitional species. The CalCOFI records obtained by Dales (1953) and McGowan (1967) for *C. japonica* showed seasonal patterns of distribution and abundance in the California Current that were basically in agreement with the results of Seapy (1974), i.e., maximal densities off southern California occurred in the summer.

Warm Water Epipelagic Species

Five of the euthecosomes and two of the heteropods collected in the present study are recognized as warm water epipelagic species, although two of the euthecosomes (*Limacina bulimoides* and *Cavolinia inflexa*) are most abundant in Central waters (Table 2). Meeting the hypothesized criterion of low abundance, the two heteropods and two of the five euthecosomes were collected in extremely low numbers (means of 0.1·10,000 m^{-3} or less). Among the three remaining euthecosomes (*Creseis virgula, Limacina bulimoides,* and *Cavolinia inflexa*), only *C. virgula* was abundant (ranking second to *Limacina helicina,* with a mean density of 228·10,000 m^{-3}), while the other two species had very low mean densities (9 and 5·10,000 m^{-3}, respectively). Classification of *C. virgula* as a warm water species is in agreement with McGowan (1967), who showed that this species was absent from California Current waters north of Point Conception. South of Point Conception, McGowan's data indicated that *C. virgula* increased in abundance from June (in offshore and southern waters) to a maximum in October (in a broad area extending to the southeast of Point Conception). In San Pedro Basin, we found that its abundance was variable during most of the year (below about 250·10,000 m^{-3}) except for higher numbers in July and a maximum in excess of 1,500·10,000 m^{-3} in August. Thus, our results support the above hypothesis of low abundance with a summertime peak occurring at the time of increased Southern California Countercurrent flow.

Limacina bulimoides is distributed primarily in Central waters (Bé & Gilmer, 1977), and is absent from the Eastern Tropical Pacific (McGowan, 1960, 1971). In his 1967 CalCOFI atlas, McGowan reported *L. bulimoides* in low numbers. Further, it was collected infrequently in offshore waters and was not recorded from nearshore waters, including the Southern California Bight. Thus, our results do not agree with those of McGowan. Although present in low numbers during most of the year in San Pedro Basin, *L. bulimoides* had elevated densities in June and August, suggesting a summertime increase when Southern California Countercurrent flow is maximal. However, the high mean density recorded in December does not fit the hypothesized seasonal pattern for epipelagic warm water species.

In the North Pacific, the range of *Cavolinia inflexa* is largely limited to subtropical latitudes, mostly in Central waters (McGowan, 1960). In the California Current, McGowan (1967) recorded it almost exclusively from waters south of Point Conception and to the south and offshore from the Southern California Bight, and the highest densities occurred in April of 1952. We recorded the highest densities of *C. inflexa* in April of 1990, although low numbers (mean monthly densities of less than 11·10,000 m^{-3}) occurred during the other months of the study.

Warm Water Mesopelagic Species

Five species (four euthecosomes and one heteropod) are included in this category. Two (*Limacina inflata* and *Clio pyramidata*) were moderately abundant in our study (the fourth and fifth ranked species, respectively), while the others were infrequently collected and had very low mean densities; 0.3·10,000 m^{-3} (*Clio cuspidata* and *Pterotrachea coronata*) and 0.1·10,000 m^{-3} (*Diacria trispinosa*). In basic agreement with our results, McGowan (1967) recorded *D. trispinosa* from a limited number of stations that were mainly in offshore waters and *C. cuspidata* at only two offshore stations, with neither species occurring off southern California. Because all of these species occur primarily in mesopelagic waters during the day and migrate into the epipelagic zone at night, the daytime data collected in our study undoubtedly represent underestimates of the true population densities.

In California Current waters ranging from central California to Baja California, McGowan (1967) recorded *Limacina inflata* as moderately to highly abundant, and during April 1950 and 1952 it occurred in Borderland waters. We found highest densities of *L. inflata* from December through March, with much lower numbers at other times of the year. Because McGowan did not include these months in his atlas, we can not compare our results with his for the same time period. Our findings of maximal densities during the winter, followed by decreasing numbers in the spring support the hypothesis that this primarily mesopelagic species becomes maximally abundant when the California Undercurrent surfaces.

Over a broad region of the California Current (from central California to southern Baja California), *Clio pyramidata* occurred patchily and mostly in low densities (McGowan, 1967). In agreement with McGowan, we found that *C. pyramidata* was present year-round and in moderately low densities (monthly means of less than 125·10,000 m^{-3}), with no evidence for a wintertime density maximum associated with surfacing of the California Undercurrent.

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